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Phylogeny of the Viperine Snakes (Viperinae): Part I. Character Analysis

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A Contribution in Celebration of the Distinguished Scholarship of Robert F. Inger on the Occasion of His Sixty-Fifth Birthday

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Grubb, P. J., J. R. Lloyd, and T. D. Pennington. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. Journal of Ecology, **51**: 567–601.

Langdon, E. J. M. 1979. Yagé among the Siona: Cultural patterns in visions, pp. 63–80. *In* Browman, D. L., and R. A. Schwarz, eds., Spirits, Shamans, and Stars. Mouton Publishers, The Hague, Netherlands.

Murra, J. 1946. The historic tribes of Ecuador, pp. 785–821. *In* Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

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Phylogeny of the Viperine Snakes (Viperinae): Part I. Character Analysis

Abstract

This paper represents the character analysis of transformation series for 55 multistate characters to be used in a subsequent cladistic study of the phylogenetic history of the Viperinae. Selection of the Azemiopinae and Crotalinae as the near outgroup and the Colubridae as a distant out-group is discussed, and polarization of transformation series is based on out-group comparison. Other criteria for identifying ancestral states when character distributions do not allow use of strict outgroup comparisons are discussed. Criteria for establishing and identifying states of continuously varying meristic and mensurate characters are proposed.

Introduction

Although it is generally agreed that the family Viperidae is a monophyletic unit (Liem et al., 1971), relationships among major lineages within this family are inadequately resolved. This lack of well-resolved relationships has seriously limited coherent discussion of patterns of evolution within this particularly interesting group of snakes. Attempts have been made to define the major groups within the Viperidae (Boulenger, 1896; Underwood, 1967; Liem et al., 1971; Dowling & Duellman, 1974–1978); these are generally in agreement, except for controversies regarding hierarchal position and possible subfamilial recognition of *Causus* with the true vipers.

Historically, the subfamily Viperinae has attracted continuous attention; however, phylogenetic resolution of included lineages has proven to be particularly difficult. The most recent attempt to discuss relationships within the Viperinae (Marx & Rabb, 1965) failed to resolve structure in relationships among major lineages. In order to further resolve these lineages, Marx and Rabb (1972) provided a detailed analysis of 50 characters shared among taxa within the superfamily Colubroidea. Definition of primitive character-states and homologous structures within a broader context limits the use of these characters in establishing relationships among lineages within the Viperinae.

Our goal in this study is to provide significant resolution of the relationships among the taxa of true vipers. As an initial step toward this end, we have undertaken to provide a rigorous analysis of pertinent character systems, based primarily on characters developed by Marx and Rabb (1972). This has required definition of a new out-group for the Viperinae, addition of 16 characters not considered in previous studies, and discussion of pertinent criteria for establishing ancestral states and ordering transformation series.

For material examined, see Part II (Ashe & Marx, 1988).

Selection

Characters

Selection of characters used in this study is based primarily on the wealth of information available on viperine and related snakes in the literature (see Marx & Rabb, 1972, and included references). In relation to these characters, we have chosen to use all available characters and to treat each as of equal weight for initial analysis. The danger that resolution of phylogenetically informative characters will be swamped by multistate characters which may have less phylogenetic information is recognized here. However, we see no meaningful way to make preconceived judgments about the nature of phylogenetic information available in any character.

Variation in many of the characters used in this study is not well understood. This primarily results from lack of adequate sample sizes in many of the taxa included. Thus, the effect of intraspecific or intrageneric variation on the character analysis cannot be properly assessed, but we recognize its importance. Of equal concern is the possibility that some of the characters included in this study may be correlated among themselves or with such variable factors as size or ontogeny. If true, then correlated characters would actually represent variations of a single character-state. Treating each of these separately would have the effect of weighting that character-state more heavily in the cladistic analysis. While we recognize this as a possibility, extensive study of correlation among character-states within viperine snakes is outside the range of this study and clearly represents a major issue in understanding character-state evolution and general evolutionary patterns within the Viperidae as a whole.

In spite of lack of complete information, it seems clear to us that initial analysis of available data for such a well-known but cladistically poorly understood group as the Viperinae is warranted at this time.

Out-Group

In this study we primarily base character analysis on an out-group composed of the subfamilies Crotalinae and Azemiopinae. However, because of the problems associated with lack of resolution of sister group relationships among subfamilies of the Viperidae, all character transformation series cannot be polarized using distribution of characters among these taxa. Therefore, we have chosen the Colubridae to provide character distribution comparisons from a more distant out-group. The Colubridae is particularly appropriate because this family has been generally assumed to form the sister group of the Viperidae, though no rigorous study of relationships among families of colubroid snakes has been published (Marx & Rabb, 1972; Kardong, 1980; Cadle, 1982).

The Crotalinae and Azemiopinae, together with the Viperinae, make up the family Viperidae. We accept the interpretation presented by Liem et al. (1971) that the Viperidae is a natural group based on the unique and highly derived structure of the feeding mechanism. However, within the Viperidae, the sister group relationships among the three included subfamilies are not clearly understood. It seems apparent that the Crotalinae represents a monophyletic group based on the unique presence among all members of the subfamily of the heat sensory pits and associated skull modifications. The Azemiopinae contains only a single species and by definition is monophyletic.

In contrast, the Viperinae as defined by Liem et al. (1971) cannot be demonstrated to be monophyletic based on known apomorphic characteristics. However, Groombridge (1984) believed that the Viperinae, less *Causus,* could be shown to be monophyletic based on a derived reversal in structure of the facial carotid artery. Test of the monophyly of the Viperinae in the above sense is one of the goals of this study. This monophyly cannot be tested until distribution of character-states and their ancestral or derived condition is hypothesized. The possibility that the Viperinae is paraphyletic or polyphyletic does not seriously compromise use of the subfamily in a traditional sense—as a working unit with the clear understanding that its limits may require modification as a result of this or additional studies.

Known derived characteristics do not allow for resolution of sister group relationships among subfamilies of the Viperidae. Sister group to the Viperinae could consist of the Azemiopinae, or the subfamily Crotalinae, or the Crotalinae and the Azemiopinae combined. Since sister group relationships among these taxa are unclear, character analysis requires either consideration of distribution of character-states among all three simultaneously or among all possible resolutions of the relationship among them. Consideration of the Colubridae as a more distant out-group provides a means of resolving the ancestral condition for those characters shared among viperids and colubrids. For character analysis, the most informative member of the out-group within the Viperidae is the subfamily Azemiopinae. While many character systems appear to show parallel evolution within the Crotalinae and Viperinae, the state found in the Azemiopinae is almost always very similar to that found among colubrids and therefore is readily resolvable as the ancestral condition.

Criteria for Interpretation

Ancestral States

Fundamental to character analysis is the resolution of the polarity of transformation among available character-states. This requires that the ancestral condition be hypothesized. The unresolved trichotomy among the three subfamilies of the Viperidae presents some interesting complications in applying the principle of out-group comparison (Watrous & Wheeler, 1981; Maddison et al., 1984). Since our goal is to determine the ancestral condition within the Viperinae, it is most easily interpreted when both the Crotalinae and Azemiopinae share a state which also occurs in the Viperinae. By any of the three possible resolutions of the trichotomy, if any two states occurring in the Viperinae also occur in the Crotalinae, application of the rules outlined in Maddison et al. (1984) show that the primitive state must be the one occurring in the monotypic Azemiopinae (fig. 1). Forty-six of the characters used in this study have this pattern of state distribution.

This method of comparison will not resolve the primitive condition in those instances in which the three subfamilies do not share a single state. In these instances comparisons with a further out-group, the Colubridae, allow for unambiguous resolution of the primitive condition among the Viperinae. In this study, nine characters fall into this category and are interpreted as follows:

A. If each subfamily of the group shares a state with the Viperinae, both the out-group states differ from each other (chars. 25, 41, 59):
   1. When the states found in the Azemiopinae and some Crotalinae are at the same end of the range of states which occur in the Viperinae, and one of these states is shared between the Azemiopinae and the Colubridae, the condition found in the Azemiopinae is used to infer the ancestral condition (chars. 25, 41);
   2. When the states found in the Azemiopinae and some Crotalinae are at opposite extremes of a range of states which occur in the Viperinae and the condition found in the Azemiopinae is also found in the Colubridae, the condition in the Azemiopinae is hypothesized to represent the ancestral state (char. 59).

B. If the out-groups have different states and only the state found in either the Azemiopinae or Crotalinae also occurs with the Viperinae (chars. 32–33, 38, 53, 65):
   1. When the Azemiopinae and the Colubridae share a state with the Viperinae and the Crotalinae has a unique state, the condition in the Azemiopinae is hypothesized to be ancestral (char. 33);
   2. When the state found in the Azemiopinae is beyond one end of a range of states found in the Viperinae and this state is shared with members of the Colubridae, and some Crotalinae have states near that same end, then the state occurring in the Viperinae which is nearest to that found in the Azemiopinae is interpreted as ancestral (chars. 38, 65);
   3. If the state in the Azemiopinae does not occur in the Viperinae but forms an extreme of a morphological gradient with states found in the Viperinae, and the state in the Azemiopinae is also found in the Colubridae, then the state in the Azemiopinae is interpreted as ancestral (char. 32);
   4. If a state in the Viperinae is shared with some Crotalinae but is not found in either the Azemiopinae or Colubridae, then that state found in both the Viperinae and Crotalinae is hypothesized to be ancestral within the Viperinae (char. 53).

C. If character information is unknown for the Azemiopinae and more than one state occurs in each of the Viperinae, Crotalinae, and Colubridae, then the state generally is taken to be ancestral for the Reptilia as a whole and is assumed to be ancestral in the Viperinae (char. 57).

Transformation Series

In discussing criteria for interpreting transformation series, we divide characters into two types, gradient and nongradient. Gradient characters consist of states that may be arrayed into a linear transformation series and are either meristic or mensurate. Polarization of these linear series is only possible by hypothesizing an ancestral condition and assuming that the transformation series

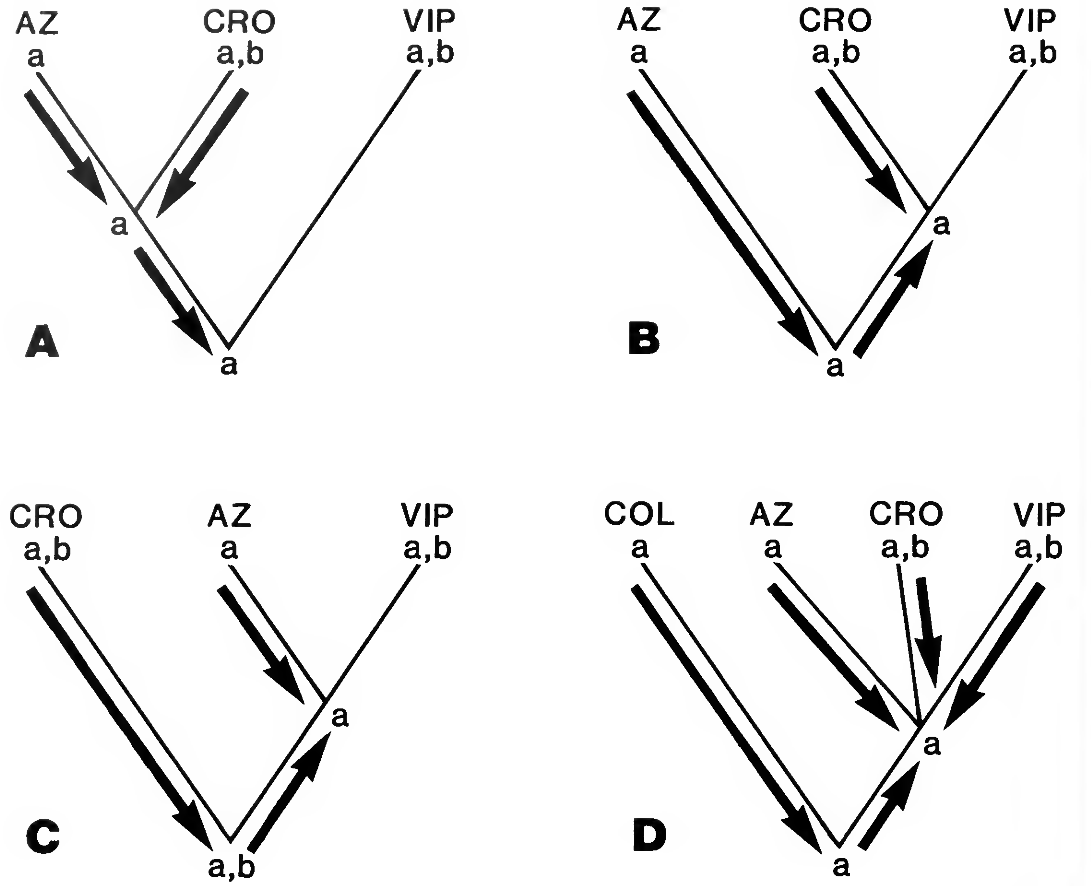

FIG. 1. Resolution of the ancestral condition of character-states for the Viperinae (VIP), using distribution of character-states in the out-groups of Azemiopinae (AZ), Crotalinae (CRO), and Colubridae (COL), based on all possible resolutions of the unresolved trichotomy of subfamily-level taxa in the Viperidae. Procedure of resolution is based on Maddison et al. (1984). **A,** Azemiopinae and Crotalinae form the sister group to Viperinae; **B,** Azemiopinae forms the sister group to Crotalinae and Viperinae; **C,** Crotalinae forms the sister group to Azemiopinae and Viperinae; and **D,** sister group relationships within the Viperidae unresolved and Colubridae (COL) used as the out-group.

is linear from this condition. We recognize that, in reality, reversals and/or nonlinear modifications are possible in such transformation series. However, no information available to us allows us to resolve such nonlinear changes. Therefore, rather than not use such characters, we choose to accept their possible limitations. Identities of gradient characters are as follows:

1. Morphological (chars. 1, 3, 7, 13, 40, 62)
2. Topographic position (char. 5)
3. Intraspecific variation (chars. 2, in part, 8, 10, 23, 28, 43, 57, 59)
4. Numerical sequence (chars. 11, 16, 20, 22, 25–26, 39, 41–42, 45, 48–50, 63, 65–66)

Nongradient characters have states that cannot be arranged in a linear series. Rather, states appear as discrete and mutually exclusive. The transformation or connectedness of nongradient characters can only be determined by the selection of an ancestral state. The remaining states are then interpreted as evolving independently from the ancestral state (chars. 2, in part, 52–53, 56).

If a character has two states in an in-group, transformation is automatically determined if one of the states also occurs in the out-group because the state occurring in the out-group must be hypothesized to be the ancestral condition. If neither state appears in the out-group, the character may then be interpreted as either a multistate gradient or as a nongradient character. For example, character 32 has two states occurring within the Viperinae. Neither of these states occurs in the out-group. The out-group state forms the ancestral end of a multistate morphological gradient with two in-group states. If the out-group state did not form a gradient with the states found in the Viperinae (nongradient character), the in-group states would be interpreted as independent evolutionary changes within the Viperinae. No examples of the latter type occurred in this study.

Assignment of States to Meristic and Mensurate Characters

Seventeen characters are based on counts or measurements. States for these characters are determined from the range of values for each species. The individual species ranges are clearly definable, and are smaller than the total range for all taxa in the study. However, individual species ranges also overlap and may form a continuum; they do not automatically segregate into discrete states. In order to assign discrete states to species ranges, the total range for all species must be partitioned. The size of the partitions is arbitrary; however, if they are too large, potentially useful information will be lost, and if they are too small, excess noise will be created.

We selected the mean of all of the individual species span of the ranges for a particular character as the partition size for that character. Taxa were assigned to states by the same rule used by Marx and Rabb (1972, p. 56). If at least two-thirds of the range of a given taxon falls between partitions, it is assigned to that corresponding state. If it does not fall between partitions by two-thirds or more, it is assigned to an intermediate state. States not found in the Viperinae are enclosed in parentheses and are not given a state number. Characters having these features are 11, 16, 20, 22, 25–26, 38–39, 41–42, 45, 48–50, 63, and 65–66.

Characters

Discussion

In order to facilitate comparisons, the number designations of characters 1–50 used in this text correspond to comparable designations in Marx and Rabb (1972). Where appropriate, detailed descriptions of some states and figures or references to figures are referred to Marx and Rabb (1972). It should be noted that, of the 66 characters discussed in the text, 11 (chars. 12, 17, 19, 29–30, 34–36, 44, and 46–47) show only a single state in the Viperinae. Invariant characters are included in the following character discussion because their importance in viperid systematics has been ascertained (Marx & Rabb, 1972), and to indicate that their relevance to studies of viperine snakes has been investigated. In addition, characters 51–66 are not considered in previous studies. General distribution of characters analyzed in this study is given in Table 1.

TABLE 1. Morphological distribution of variable and invariant characters examined in viperine snakes.

Region	Variable	Invariant	Total
Head	21	1	22
Skull	24	8	32
Body	6	2	8
Tail	3	0	3
Reproduction	1	0	1
Total	55	11	66

We are aware that the conventional designation of the ancestral condition is referred to as "state 0." However, we have chosen to depart from convention for the following reasons: Many characters have states that form a numerical sequence. When listed in sequence, the ancestral state may not be at the extremes of this series. Therefore, use of a "0" to denote an extreme condition would incorrectly imply an ancestral position. In addition, this provides cross-reference to character-states used in Marx and Rabb (1972), on which we have relied.

Description

CHARACTER 1: DORSAL HEAD SCALATION

State 1—9 head shields
State 2—some large shields, some small scales
State 3—all small scales

State 1 occurs in *Azemiops*, some Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. Partial fragmentation of head shields (state 2) is interpreted as morphologically intermediate between states 1 and 3.

Character transformation is interpreted as 1 → 2 → 3.

CHARACTER 2: ROSTRAL SHIELD

State 1—single and rounded
State 2—single, large, and modified

State 3—intraspecific variation between states 1 and 4
State 4—fragmented into several scales

State 1 occurs in *Azemiops,* in some Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. State 2 represents an independent modification of the rostral shield which among viperines is found only in the genus *Causus.* State 3 is interpreted as intermediate between states 1 and 4 based on the criterion of intraspecific variation.

Character transformation is interpreted as 2 ← 1 → 3 → 4.

Character 3: Position of Nasal Shield

State 1—in contact with rostral and supralabials
State 2—separated from supralabials, but in contact with rostral
State 3—separated from rostral and supralabials

State 1 occurs in *Azemiops,* all Crotalinae, and most Colubridae. Based on an out-group comparison, state 1 is interpreted as the ancestral state. State 2 is interpreted as morphologically intermediate between states 1 and 3.

Character transformation is interpreted as 1 → 2 → 3.

Character 4: Nasal Shield Depression

State 1—absent
State 2—present

State 1 occurs in *Azemiops* and in all Crotalinae. Based on out-group comparison, state 1 is interpreted as the primitive state.

Character transformation is interpreted as 1 → 2.

Character 5: Position of Nostril in Nasal Shield

State 1—medial
State 2—anterior
State 3—posterior

State 1 occurs in *Azemiops,* most Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. Since the primitive state is intermediate topographically, we interpret states 2 and 3 as independent derivations.

Character transformation is interpreted as 2 ← 1 → 3.

Character 6: Supranasal Horns

State 1—absent
State 2—present

State 1 occurs in *Azemiops,* all Crotalinae, and all Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 7: Loreal Shields

State 1—1
State 2—more than 3
State 3—absent

State 1 occurs in *Azemiops,* some Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. Within the Viperinae, state 3 occurs only in the monotypic genus *Adenorhinos.* Since *Adenorhinos* exhibits scale fragmentation on other regions of the head and overall reduction in number of head shields, we interpret the absence of loreals (state 3) to be a modification of state 2.

Character transformation is interpreted as 1 → 2 → 3.

Character 8: Supraocular Horns

State 1—absent
State 2—intraspecific variation
State 3—present

State 1 occurs in *Azemiops,* most Crotalinae, and all Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. State 2 is interpreted as intermediate between states 1 and 3 based on the criterion of intraspecific variation.

Character transformation is interpreted as 1 → 2 → 3.

Character 9: Anterior Temporal Shields

State 1—1–3
State 2—more than 3

State 1 occurs in *Azemiops,* some Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 10: Interoculabials

State 1—absent
State 2—intraspecific variation
State 3—present

State 1 occurs in *Azemiops,* some Crotalinae, and all Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. State 2 is interpreted as intermediate between states 1 and 3 based on the criterion of intraspecific variation.

Character transformation is interpreted as 1 → 2 → 3.

CHARACTER 11: NUMBER OF SUPRALABIALS

The range of supralabials in Viperinae is 5–18.

State 1—5–7
State 2—intermediate
State 3—8–10
State 4—intermediate
State 5—11–13
State 6—intermediate
State 7—14–16
State 8—intermediate
—(17–19)*

State 1 occurs in *Azemiops,* some Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. States 1–8 are interpreted as a linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 → 2 → 3 . . . → 8.

CHARACTER 12: EYE POSITION TO SUPRALABIALS

All Viperinae have the supralabials separated from the eye.

CHARACTER 13: EYE SIZE

State 1—moderate
State 2—small
State 3—large

See Marx and Rabb (1972) for description of states.

State 1 occurs in *Azemiops,* most Crotalinae, and many Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. Since the ancestral state is morphologically intermediate, states 2 and 3 are interpreted as independent changes.

Character transformation is interpreted as 2 ← 1 → 3.

* Here and elsewhere, character-states not found in the Viperinae are not assigned character-states; however, they are shown to fix the ranges of the series.

CHARACTER 14: MIDTHROAT SCALATION

State 1—midline is occupied by larger chin shields (Marx & Rabb, 1965, figs. 41D,H)
State 2—midline is occupied by numerous gular scales (Marx & Rabb, 1965, fig. 41F)

State 1 occurs in *Azemiops,* many Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

CHARACTER 15: CARINATION OF GULAR SCALES

State 1—smooth (Marx & Rabb, 1965, fig. 41F)
State 2—keeled (Marx & Rabb, 1965, fig. 41H)

State 1 occurs in *Azemiops,* most Crotalinae, and all Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

CHARACTER 16: NUMBER OF SCALE ROWS AT MIDBODY

The range in Viperinae is 15–41.

State 1—15–18
State 2—intermediate
State 3—19–22
State 4—intermediate
State 5—23–26
State 6—intermediate
State 7—27–30
State 8—intermediate
State 9—31–34
State 10—intermediate
State 11—35–38
State 12—intermediate
—(39–42)

State 1 occurs in *Azemiops,* some Crotalinae, and many Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. States 1–12 are interpreted as a linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 → 2 → 3 . . . → 12.

CHARACTER 17: DORSAL SCALES SMOOTH OR KEELED

All Viperinae have keeled dorsal scales.

Character 18: Serrated Keels on Lateral Scales

State 1—absent
State 2—present

State 1 occurs in *Azemiops,* most Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.
Character transformation is interpreted as 1 → 2.

Character 19: Apical Pits

All Viperinae have apical pits on dorsal scales.

Character 20: Number of Ventrals

The range in Viperinae is 102–205.

State 1—102–123
State 2—intermediate
State 3—124–145
State 4—intermediate
State 5—146–167
State 6—intermediate
State 7—168–189 (out-group only)
State 8—intermediate

State 7 occurs in *Azemiops,* some Crotalinae, and most Colubridae. Based on out-group comparison, state 7 is interpreted as the ancestral state. States 1–8 are interpreted as a linear series by the criterion of numerical sequence. State 7 does not occur in the Viperinae; however, it serves to root the transformation series for this bidirectional character.
Character transformation is interpreted as 8 ← (7) → 6 → 5 → 4 → 3 → 2 → 1.

Character 21: Keeling on Ventral Shields

State 1—unkeeled
State 2—keeled

State 1 occurs in *Azemiops,* all Crotalinae, and many Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.
Character transformation is interpreted as 1 → 2.

Character 22: Number of Subcaudals

The range in Viperinae is 10–65.

State 1—10–23
State 2—intermediate
State 3—24–37
State 4—intermediate
State 5—38–51
State 6—intermediate
State 7—52–65

State 5 occurs in *Azemiops,* some Crotalinae, and many Colubridae. Based on out-group comparison, state 5 is interpreted as the ancestral state. States 5–1 and states 5–7 are interpreted as linear series by the criterion of numerical sequence.
Character transformation is interpreted as 7 ← 6 ← 5 → 4 → 3 → 2 → 1.

Character 23: Keeling of Subcaudal Shields

State 1—unkeeled
State 2—intraspecific variation
State 3—keeled

State 1 occurs in *Azemiops,* all Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. State 2 is interpreted as intermediate between states 1 and 3 by the criterion of intraspecific variation.
Character transformation is interpreted as 1 → 2 → 3.

Character 24: Subcaudals Paired or Single

State 1—paired
State 2—single

State 1 occurs in *Azemiops,* some Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.
Character transformation is interpreted as 1 → 2.

Character 25: Relative Length of Anterior Portion of Skull

The range in Viperinae is 38.7%–62.8%.

—(38.7%–41.1%)
State 1—intermediate
—(41.2%–43.6%)
State 2—intermediate
State 3—43.7%–46.1%
State 4—intermediate
State 5—46.2%–48.6%
State 6—intermediate
State 7—48.7%–51.1%
State 8—intermediate
State 9—51.2%–53.6%
State 10—intermediate
State 11—53.7%–56.1%
State 12—56.2%–58.6%

State 2 occurs in *Azemiops,* and states 3–11 occur in the Crotalinae. Based on the condition in most Colubridae, we conclude that the lower range of the relative length of the anterior portion of the skull is the more primitive. Since state 2 occurs in *Azemiops,* we interpret that state as ancestral. States 2–12 are interpreted as a linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 → 3 → 4 . . . → 12.

Character 26: Relative Width of Skull

The range in Viperinae is 20.3%–60.6%.

State 1—20.3%–23.1%
State 2—26.1%–28.9%
State 3—intermediate
State 4—29.0%–31.8%
State 5—intermediate
State 6—31.9%–34.7%
State 7—34.8%–37.6%
State 8—37.7%–40.5%
—(40.6%–43.4%)
State 9—intermediate
State 10—43.5%–46.3%
—(46.4%–49.2%)
State 11—intermediate
—(49.3%–52.1%)

State 4 occurs in *Azemiops,* some Crotalinae, and most Colubridae. Based on out-group comparison, state 4 is interpreted as the ancestral state. States 4–1 and 4–11 are interpreted as linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 ← 3 ← 4 → 5 → 6 . . . → 11.

Character 27: Posterior Process of Lateral Arms of Premaxilla

State 1—absent
State 2—present

State 1 occurs in *Azemiops,* all Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 28: Vomer Ring

State 1—lamina fenestrated, ring complete
State 2—intraspecific variation
State 3—lamina deeply emarginated (ring complete) or part of lamina absent

State 1 occurs in *Azemiops,* many Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. State 2 is interpreted as intermediate between states 1 and 3 by the criterion of intraspecific variation.

Character transformation is interpreted as 1 → 2 → 3.

Character 29: Lateral Process of Palatine

All Viperinae lack the lateral process of the palatine.

Character 30: Maxillary Nerve Foramen in Palatine Bone

Not applicable to Viperinae.

Character 31: Palatine-Pterygoid Articulation

State 1—both bones notched, a saddle joint
State 2—overlap joint

State 1 occurs in *Azemiops,* many Crotalinae, and some Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. By analyzing this character in reference to a more restricted group, the Viperidae, we reverse the polarity from that given by Marx and Rabb (1972). They based a polarity decision on a trend from simple to complex. Based on character-state distribution within the Viperidae, it is not possible to defend the proposition that state 2 is the ancestral condition within the Viperinae.

Character transformation is interpreted as 1 → 2.

Character 32: Medial Wing of Prefrontal

State X—present, well developed
State 1—present, small
State 2—absent

Neither of the states present in the Viperinae occurs in *Azemiops.* Azemiopinae, as well as many Colubridae, have the medial wing of the prefrontal well developed (state X). However, state 1 is interpreted as ancestral within the Viperinae, since it is morphologically intermediate between the condition in *Azemiops* and state 2. State 1 also occurs in some Crotalinae.

Character transformation is interpreted as X → 1 → 2.

Character 33: Dorsal Processes of Prefrontal

State 1—medial and posterior dorsal processes present
State 2—posterior dorsal process absent

State 1 occurs in *Azemiops* and a few Colubridae; however, crotalines have the prefrontal process short and knobby, a condition unique to that subfamily. State 1 is interpreted as ancestral based on criterion B-1.

Character transformation is interpreted as 1 → 2.

Character 34: Anterolateral Wing of Frontal Bone

The anterolateral wing of the frontal bone is present in all Viperinae.

Character 35: Postorbital Bone

The postorbital bone is present in all Viperinae.

Character 36: Anterolateral Process of Parietal

The anterolateral process of the parietal is absent in all Viperinae.

Character 37: Parietal Bone

State 1—bulbous anteriorly
State 2—moderately bulbous overall

State 1 occurs in *Azemiops,* some Crotalinae, and many Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 38: Relative Length of Quadrate

The range in Viperinae is 27.8%–82.3%.

State X—27.8%–33.2%
State 1—33.3%–38.7%
State 2—intermediate
State 3—38.8%–44.2%
State 4—44.3%–49.7%
State 5—intermediate
State 6—49.8%–55.2%
State 7—intermediate
State 8—55.3%–60.7%
State 9—60.8%–66.2%
State 10—intermediate
State 11—66.3%–71.7%
State 12—intermediate —(71.8%–77.2%)

The condition in *Azemiops* (27.3%–31.8%) is immediately below the range of state 1 within the Viperinae (state X). Some Crotalinae (certain species of *Agkistrodon*) and most Colubridae fall within the lower range of states (states 1–6) found within the Viperinae. We conclude that the lowest relative length (state 1) of the Viperinae is the most ancestral state. States 1–12 are interpreted as a linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 → 2 → 3 . . . → 12.

Character 39: Relative Length of Squamosal to Skull Length

The range in Viperinae is 22.7%–42.6%.

State 1—22.7%–25.4%
State 2—intermediate
State 3—25.5%–28.2%
State 4—intermediate
State 5—28.3%–31.0%
State 6—intermediate
State 7—31.1%–33.8%
State 8—intermediate
State 9—33.9%–36.6%
State 10—intermediate
State 11—36.7%–39.4%
State 12—intermediate —(39.5%–42.2%)

State 3 occurs in *Azemiops,* some Crotalinae, and most Colubridae. Based on out-group comparison, state 3 is interpreted as the ancestral state. The remainder of the states are ordered by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 ← 3 → 4 → 5 . . . → 12.

Character 40: Compound Processes

State 1—1, medial
State 2—2, medial larger
State 3—2, equal size

State 1 occurs in *Azemiops,* all Crotalinae, and many Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. This character reflects a trend of gradual increase in the size of the lateral process of the compound. State 2 is interpreted as morphologically intermediate.

Character transformation is interpeted as 1 → 2 → 3.

Character 41: Relative Length of Compound

The range in Viperinae is 54.3%–114.8%.

State 1—54.3%–59.7%
State 2—59.8%–65.2%
State 3—65.3%–70.7%
State 4—70.8%–76.2%
State 5—76.3%–81.7%
State 6—intermediate
State 7—81.8%–87.2%
State 8—87.3%–92.7%
State 9—92.8%–98.2%
State 10—intermediate
—(98.3%–103.7%)
State 11—103.8%–109.2%

State 2 occurs in *Azemiops* and many Colubridae. However, states 5–11 occur within the Crotalinae. Since some Crotalinae (*Agkistrodon*) have a relatively short compound, state 2 is interpreted as ancestral for the Viperinae. The remainder of the states are ordered by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 → 3 → 4 . . . → 11.

Character 42: Relative Length of Dentary

The range in Viperinae is 35.9%–70.9%.

State 1—35.9%–40.4%
State 2—40.5%–45.0%
State 3—45.1%–49.6%
State 4—intermediate
State 5—49.7%–54.2%
State 6—intermediate
State 7—54.3%–58.8%
State 8—intermediate
State 9—58.9%–63.4%
State 10—intermediate
State 11—63.5%–68.0%

State 5 occurs in *Azemiops,* some Crotalinae, and many Colubridae. Based on out-group comparison, state 5 is interpreted as the ancestral state. The complete range of states within the Viperinae is also found within the Crotalinae. However, some Crotalinae (*Agkistrodon*) possess character-states similar to those of *Azemiops.* The remainder of the states are ordered by the criterion of numerical sequence.

Character transformation is interpreted as 1 . . . ← 4 ← 5 → . . . → 11.

Character 43: Presence of Splenial and Angular Bones

State 1—2 present
State 2—intraspecific variation
State 3—1 present

State 1 occurs in *Azemiops,* many Crotalinae, and most Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. State 2 is interpreted as intermediate between states 1 and 3 by the criterion of intraspecific variation.

Character transformation is interpreted as 1 → 2 → 3.

Character 44: Number of Maxillary Teeth

All Viperinae have a single maxillary tooth.

Character 45: Relative Length of Longest Maxillary Tooth

The range in Viperinae is 13.3%–60.3%.

State 1—13.3%–16.9%
State 2—17.0%–20.6%
State 3—20.7%–24.3%
State 4—24.4%–28.0%
State 5—28.1%–31.7%
State 6—intermediate
State 7—31.8%–35.4%
State 8—intermediate
State 9—35.5%–39.1%
State 10—intermediate
State 11—39.2%–42.8%
State 12—intermediate
—(42.9%–46.5%)
State 13—intermediate
—(46.6%–50.2%)
State 14—50.3%–53.9%

State 3 occurs in *Azemiops,* some Crotalinae, and some Colubridae. Based on out-group comparison, state 3 is interpreted as the ancestral state. States 3–1 and states 3–14 are interpreted as linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 ← 3 → 4 → 5 . . . → 14.

Character 46: Position of Fangs and Their Groove

All Viperinae have fangs positioned posteriorly and grooved anteriorly.

CHARACTER 47: POSITION OF ENLARGED MAXILLARY TEETH

All Viperinae have an enlarged maxillary tooth positioned posteriorly.

CHARACTER 48: NUMBER OF PALATINE TEETH

The range in Viperinae is 0–9.

State 1—0–1.49
State 2—intermediate
State 3—1.50–2.99
State 4—intermediate
State 5—3.00–4.49
State 6—4.50–5.99
—(6.00–7.49)
State 7—intermediate
State 8—7.50–8.99

State 5 occurs in *Azemiops*, some Crotalinae, and some Colubridae. Based on out-group comparison, state 5 is interpreted as the ancestral state. States 5–1 and states 5–8 are interpreted as linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← . . . 4 ← 5 → 6 → 7 → 8.

CHARACTER 49: NUMBER OF PTERYGOID TEETH

The range in Viperinae is 8–32.

State 1—8–11
State 2—intermediate
State 3—12–15
State 4—intermediate
State 5—16–19
State 6—intermediate
State 7—20–23
State 8—intermediate
State 9—24–27
State 10—28–31
State 11—32

State 3 occurs in *Azemiops*, some Crotalinae, and many Colubridae. Based on out-group comparison, state 3 is interpreted as the ancestral state. States 3–1 and states 3–11 are interpreted as linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 ← 3 → 4 → 5 . . . → 11.

CHARACTER 50: NUMBER OF DENTARY TEETH

The range in Viperinae is 11–29.

State 1—11–14
State 2—intermediate
State 3—15–18
State 4—intermediate
State 5—19–22
State 6—intermediate
State 7—23–26
State 8—27–29

State 3 occurs in *Azemiops*, some Crotalinae, and most Colubridae. Based on out-group comparison, state 3 is interpreted as the primitive state. States 3–1 and 3–8 are interpreted as linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 ← 3 → 4 → 5 → 6 → 7 → 8.

CHARACTER 51: POSITION OF PARIETAL RELATIVE TO POSTORBITAL BONE

The parietal and postorbital bones are in contact with each other in two different positions (see Marx & Rabb, 1965, pp. 163–164).

State 1—contact posterior (Marx & Rabb, 1965, fig. 32)
State 2—contact medial (Marx & Rabb, 1965, fig. 33)

State 1 occurs in *Azemiops* and all Crotalinae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

CHARACTER 52: POSTERODORSAL PROJECTION OF THE PREMAXILLA

State 1—narrow (Marx & Rabb, 1965, fig. 39B)
State 2—broad (Marx & Rabb, 1965, fig. 39A)
State 3—base expanded

The anterior view of the posterodorsal projection of the premaxilla is highly variable. State 1 occurs in *Azemiops* and in some Crotalinae. Based on out-group comparison, state 1 is interpreted as the ancestral state. Neither state 2 nor state 3 appears to be morphologically intermediate. They are, therefore, interpreted to be independent modifications.

Character transformation is interpreted as 2 ← 1 → 3.

CHARACTER 53: ANTERODORSAL SHAPE OF ECTOPTERYGOID BONE

The anterodorsal shape of the ectopterygoid bone is highly variable, even within small groups of snakes (Brattstrom, 1964, figs. 29–30; Downs, 1967, fig. 2; Marx & Rabb, 1965, fig. 42). Within the Viperinae, we recognize four shapes.

State 1—lateral flange absent (Marx & Rabb, 1965, fig. 42, left)
State 2—broad lateral flange and spine (Marx & Rabb, 1965, figs. 42, center, 43)
State 3—narrow lateral flange and spine (Lombard et al., 1986, fig. 2K)
State 4—broad in center without spine (Marx & Rabb, 1965, fig. 42, right)

Within the out-group, consisting of *Azemiops* and Crotalinae, a single species (*Agkistrodon strauchi*) of 45 sampled taxa shares state 1 with some Viperinae. States 2–4 do not occur in any of the out-group taxa. The ectopterygoid of *Azemiops* differs significantly from any other viperid. We therefore conclude, with reservation, that state 1 is ancestral. States 2–4 do not form a morphological gradient, and we therefore interpret states 2-4 as independent evolutionary directions.

Character transformation is interpreted as

$$\begin{array}{c} 4 \\ \uparrow \\ 2 \leftarrow 1 \rightarrow 3. \end{array}$$

Character 54: Pupil Shape

Snake eyes within the Viperinae have pupils shaped as follows:

State 1—vertically elliptical
State 2—round

State 1 occurs in *Azemiops,* all Crotalinae, and some Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 55: Supranasal Sac

A well-developed supranasal sac exists in some species of true vipers (Smith, 1943; Marx & Rabb, 1965).

State 1—absent
State 2—present

State 1 occurs in *Azemiops* and in some Crotalinae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 56: Lateral Body Scale Rows

The lateral body scale rows may be arranged in three patterns as follows:

State 1—angulate to body axis, not oblique (Villiers, 1950, fig. 5).
State 2—angulate to body axis, oblique (Villiers, 1950, fig. 6)
State 3—perpendicular to body axis (Marx & Rabb, 1965, fig. 37, upper)

State 1 occurs in *Azemiops,* some Crotalinae, and some Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state. States 2 and 3 involve morphological changes in opposite directions and are interpreted as independently derived.

Character transformation is interpreted as 2 ← 1 → 3.

Character 57: Mode of Reproduction

Within the Viperinae three states are recognized.

State 1—oviparous
State 2—intraspecific variation
State 3—ovoviviparous

Ovoviviparity has evolved repeatedly in many groups of reptiles (Fitch, 1970; Tinkle & Gibbons, 1977). Both states 1 and 3 occur within the Crotalinae and Colubridae (Fitch, 1970). The condition of *Azemiops* is unknown (Zhao & Zhao, 1981). We therefore cannot infer the ancestral state from out-group comparison among these taxa. However, based on the distribution of these states within the reptiles as a whole, we make the assumption that egg laying (state 1) is ancestral. State 2 is interpreted as intermediate based on the criterion of intraspecific variation.

Character transformation is interpreted as 1 → 2 → 3.

Character 58: Head Distinct from Neck

The head of snakes may be distinct or not (or slightly) distinct from the neck. Two states are recognized, as follows:

State 1—not or slightly distinct
State 2—distinct (Marx & Rabb, 1965, fig. 35 A,C)

State 1 occurs in *Azemiops,* some Crotalinae, and some Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpeted as 1 → 2.

Character 59: Number of Scales Composing Nasal Shield

The nostril is located in the nasal shield. The shield may be entire or divided into two or more scales. We recognize three states as follows:

State 1—1, may be partly divided
State 2—intraspecific variation
State 3—2 or 3

Azemiops and many Colubridae and some Crotalinae have state 1. We therefore accept state 1 to be ancestral. State 2 is interpreted as intermediate based on the criterion of intraspecific variation.

Character transformation is interpreted as 1 → 2 → 3.

Character 60: Shape of Dorsal Scales

Dorsal scales are of two shapes as follows:

State 1—oval
State 2—squarish

State 1 occurs in *Azemiops,* some Crotalinae, and many Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 61: Keeling of Temporal Scales

Two states are recognized:

State 1—smooth (Marx & Rabb, 1965, fig. 41C)
State 2—keeled (Marx & Rabb, 1965, fig. 41G)

State 1 occurs in *Azemiops,* some Crotalinae, and many Colubridae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 62: Scales between Rostral and Nasal Shields

State 1—rostral in contact with nasal
State 2—1 large scale between rostral and nasal
State 3—multiple small scales between rostral and nasal

State 1 occurs in *Azemiops,* some Crotalinae and most Colubridae. Based on out-group comparison, it is interpreted as the ancestral state. State 2 is interpreted as a morphological intermediate between states 1 and 3.

Character transformation is interpreted as 1 → 2 → 3.

Character 63: Number of Shields Composing Ocular Ring

The ocular ring is defined as the total number of shields in contact with the eye. Within the Viperinae, the ocular ring may be composed of combinations of the preocular(s), supraocular, postocular(s), and supralabial(s). The range in Viperinae is 4–24.

State 1—4–5
State 2—intermediate
State 3—6–7
State 4—8–9
State 5—10–11
State 6—intermediate
State 7—12–13
State 8—intermediate
State 9—14–15
State 10—intermediate
State 11—16–17
State 12—intermediate
State 13—18–19
State 14—intermediate
—(20–21; 22–23)

State 3 occurs in *Azemiops* and in some Crotalinae. Based on out-group comparison, state 3 is interpreted as the ancestral state. States 3–1 and states 3–14 are interpreted as a linear series by the criterion of numerical sequence.

Character transformation is interpreted as 1 ← 2 ← 3 → 4 → 5 . . . → 14.

Character 64: Shape of Postorbital Bone

Within the Viperinae there are two shapes of the postorbital, as figured by Marx and Rabb (1965, figs. 32–33).

State 1—slender
State 2—broad

State 1 occurs in *Azemiops* and in all Crotalinae. Based on out-group comparison, state 1 is interpreted as the ancestral state.

Character transformation is interpreted as 1 → 2.

Character 65: Relative Length of Squamosal to Distance from Postorbital Bone

This character is defined by the length of the squamosal relative to the distance between the squamosal and the postorbital. The range in Viperinae is 93.3%–3.2%.

State 1—91.2%–95.5%
State 2—78.0%–82.3%
State 3—73.6%–77.9%
State 4—intermediate
State 5—69.2%–73.5%
State 6—intermediate (state 5; 64.8%–69.1%)
State 7—60.4%–64.7%
State 8—56.0%–60.3%
State 9—51.6%–55.9%
State 10—47.2%–51.5%
State 11—42.8%–47.1%
State 12—intermediate
State 13—38.4%–42.7%
State 14—29.6%–33.9%
State 15—intermediate
State 16—25.2%–29.5%
State 17—20.8%–25.1%
—(16.4%–20.7%)
State 18—intermediate
State 19—12.0%–16.3%
State 20—intermediate (state 21; 7.6%–11.9%)
State 21—3.2%–7.5%

The condition in *Azemiops* (108.6%–112.9%) is below the range of state 1 within the Viperinae. Some Crotalinae (certain species of *Agkistrodon*) fall within the lower range of states (states 3–7) found within the Viperinae. We conclude that the highest relative length (state 1) of the Viperinae is the ancestral state. States 1 to 21 are interpreted as a linear series by the criterion of numerical sequence. A similar interpretation is found in character 38.

Character transformation is interpreted as 1 → 2 → 3 . . . → 21.

Character 66: Relative Length of Frontal Suture

The frontal suture is the anterodorsal suture dividing the frontal bone on its midline. The relative length of the frontal suture is defined as the distance between the squamosal and postorbital as compared to the length of frontal suture. The range in Viperinae is 4.6%–153.5%.

State 1—4.6%–12.5%
State 2—intermediate (state 1; 12.6%–20.5%)
State 3—20.6%–28.5%
State 4—28.6%–36.5%
State 5—36.6%–44.5%
State 6—52.6%–60.5%
State 7—76.6%–84.5%
State 8—intermediate
State 9—84.6%–92.5%
State 10—92.6%–100.5%
State 11—intermediate (state 10; 100.6%–108.5%)
State 12—108.6%–116.5%
State 13—116.6%–124.5%
State 14—132.6%–140.5%
State 15—intermediate (state 14; 140.6%–148.5%)

State 12 occurs in *Azemiops* and in some Crotalinae. Based on out-group comparison, state 12 is interpreted as the ancestral state. States 12–1 and 12–15 are interpreted as a linear series based on the criterion of numerical sequence.

Character transformation is interpreted as 15 ← 14 ← 13 ← 12 → 11 → 10 . . . → 1.

Summary

This study provides phyletic analysis of 55 multistate characters in the viperid subfamily Viperinae. This array of characters is then applied to a cladistic analysis of viperine taxa (Ashe & Marx, 1988, Part II) based on the species as the operational taxonomic unit. These characters are, in all but one instance, morphological from the head, body, tail, and skull; a single character is based on mode of reproduction. Morphological characters include states based on position, shape, ornamentation, measurements, and numerical counts.

We believe that this diversity of kinds of characters will ultimately provide insight into origin and hierarchal significance of features among viperine snakes. Furthermore, they may make it possible to distinguish among character-state distributions resulting from various processes, including random events, speciation, history, and adaptation. Character complexes related to internal anatomy, physiology, venom characteristics, and similar functional systems, though expected to include phylogenetically informative features, were not considered in this study because of lack of sufficient comparative information among taxa considered.

In this paper, we present critical discussion of various phyletic applications of included characters. Selection of the out-group is of paramount importance to character analysis. Because the sister group of the Viperinae is not clear, we chose all other members of the family Viperidae, the Azemiopinae and Crotalinae, as initial out-group for subsequent analysis with the Colubridae chosen for broader comparisons. The primitive state of transformation series is established by distribution of character-states among members of the Viperinae and out-groups. Since some character-state distributions provide more reliable information about the primitive condition, criteria for ranking decisions about direction of character transformation are provided. Data on distribution of character-states among subfamilies of the Viperidae are based on taxa listed in Marx and Rabb (1972, pp. 309–310).

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